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DOES AGE INFLUENCE TERRITORY SIZE, HABITAT SELECTION, AND REPRODUCTIVE SUCCESS OF MALE CANADA WARBLERS IN CENTRAL NEW HAMPSHIRE?

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ABSTRACT.—The Canada Warbler (*Wilsonia canadensis*) is currently in decline in the northeastern United States and basic demographic parameters remain to be described. We studied marked populations (76 ASYs, 14 SYs, and 2 of unknown age) of Canada Warblers on two study sites from 2003 to 2006. We mapped 92 territories (including males returning in multiple years) of 71 males using handheld GPS and ArcMap. We compared the pairing and fledging success of older and younger males on both sites, a red maple (*Acer rubrum*) swamp and a young forest intensively harvested in 1985 with ~10% residual standing trees used by males as song perch trees. Both sites had a high proportion of ASYs (84% ASY for all territorial males, 77.5% of all males including non-territorial individuals). Both pairing (91%) and fledging (78%) success was comparatively high suggesting these two sites were of high value to this species. A higher proportion of SYs were transients. Pairing success was lower for younger males which established territories, but paired SYs fledged at least one young at a rate comparable to older males. This study corroborates the benefits of age and experience to reproductive performance. The results suggest that both red maple swamps and post-harvest forests with thick subcanopy vegetation and emergent trees provide high quality habitat for breeding Canada Warblers. Received 11 July 2007. Accepted 12 November 2007.

Demographic studies are important in understanding the population ecology of a bird species, especially during the breeding season. A bird's age can greatly affect its ability to hold high quality territories, pair, and successfully raise young (e.g., Ficken and Ficken 1966, Holmes et al. 1996). Older age and greater experience of males are often associated with higher reproductive performance. This has been shown for a diversity of bird species from several different families. Males with older male Great Tits (*Parus major*) laid earlier, fledged more young, and their fledglings survived at higher rates, although age of the male did not affect clutch size (Perrins and McCleery 1985). Age of the European Pied Flycatcher (*Ficedula hypoleuca*) was similarly correlated with laying date and fledgling survivorship, and older males also had greater clutch sizes (Harvey et al. 1985). Nol and Smith (1987) found that older Song Sparrows (*Melospiza melodia*) began breeding earlier and raised more young to independence than younger Song Sparrows.

The effects of age on territory quality and reproductive success have been frequently studied among Parulidae. Habitat features and/or food availability affect individual bird territory quality, which in turn influences territory size, site fidelity, and reproductive success; older males disproportionately occupy higher quality habitat (e.g., Rodenhouse and Holmes 1992). The age of Ovenbirds (*Seiurus aurocapilla*) positively correlates with habitat quality and pairing success. Older males acquire higher quality habitats and pair at higher rates than younger males (Bayne and Hobson 2001). Holmes et al. (1996) found that older Black-throated blue Warblers (*Dendroica caerulescens*) occurred in areas with higher shrub density and fledged significantly more young. Older males also returned at higher rates than yearlings and had significantly smaller territory sizes. Older American Redstart (*Setophaga ruticilla*) males arrive earlier, and pair and fledge young at higher rates than first year males. Older males also relegate first year males to less optimal breeding habitat (Sherry and Holmes 1989). These findings indicate that habitat variables and age may influence breeding success and return rates of warblers.

Understanding the relationship between age and reproductive performance and how age

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structure differs among habitats provides the needed tools for management, especially for species with documented declines. Habitat type is not a reliable predictor of reproductive success (Van Horne 1983, Vickery et al. 1992), but demographic patterns among different habitats within a species' distribution indicate age-related effects. Younger birds are often displaced into lower quality habitat where they are incapable of attracting a mate or raising young (e.g., Holmes et al. 1996, Zannette 2001). This is consistent with age-specific models of habitat selection that suggest older birds assert dominance over younger birds and secure the best habitat and, consequently, have higher fitness (e.g., Holmes et al. 1996, Hunt 1996).

This study focused on the Canada Warbler (*Wilsonia canadensis*), a small (10–12 g) Neotropical-Nearctic migrant. The Canada Warbler breeds in areas with high shrub density, such as red maple (*Acer rubrum*) swamps and young upland forest (Titterton et al. 1979, Hagan et al. 1997, Golet et al. 2001). It occurs in both early-successional forest stands and within the deciduous (DeGraaf et al. 1998) and mixed-species understories of mature forests in New Hampshire during the breeding season. The species' population is in a 2.7–4.6% per year decline over the last four decades in the region that includes this study, as estimated from North American Breeding Bird Survey data (Sauer et al. 2005). The reasons for this decline are poorly understood as few studies have been performed at the level of the individual or population. Most studies involving the Canada Warbler have been conducted at the community level, involving censuses in differing habitats. This study compares age-related habitat selection and breeding success in both naturally occurring red maple swamps and young upland forest, clear-cut in 1985 with residual tree retention.

The objectives of this study were to examine differences in the habitat characteristics, breeding success, and territory sizes between after-second-year (ASY) and second-year (SY) males within the same breeding population. We predicted these measures will show consistent patterns similar to those documented with other species. Older birds were predicted to have smaller territories, and high-

er pairing and fledging success consistent with age-based dominance-hierarchical models.

METHODS

Study Site.—This study was conducted in Canaan, New Hampshire (43° 40' N, 72° 03' W) on the Canaan Town Forest (40 ha, hereafter referred to as the lower plot) and the adjacent Bear Pond Natural Area (BPNA) (363 ha, hereafter referred to as the upper plot) (Fig. 1). The lower plot is a 40-ha red maple swamp dominated by balsam fir (*Abies balsamea*), red spruce (*Picea rubens*), and red maple with interspersed mixed upland forest. The upper plot (all within BPNA) is a 43-ha mixed deciduous upland forest, which was heavily harvested in 1985. Young regrowth dominated the harvest zone; remnant non-merchantable trees emerge from the regenerating layer as scattered individuals and in clumps. Trees (≥ 8.0 cm dbh) of the upper plot were dominated by red maple, balsam fir, eastern hemlock (*Tsuga canadensis*), red spruce, and big-toothed aspen (*Populus grandidentata*). Balsam fir dominated the smallest size class of shrubs and saplings (< 2.5 cm dbh) on the upper plot followed by *Ilex* and *Viburnum* spp., white birch (*Betula papyrifera*), and red maple.

Characterizing Male Territories.—Seventy-one territorial males were captured from 2003 to 2006 using playback of songs and calls. All birds were uniquely color-banded. Birds were assigned to age classes following plumage characteristics, i.e., molt limits of the outer primary coverts, and boldness and extent of the necklace (Rappole 1983, Pyle 1997). Male territories were mapped from 27 May to 10 July each year. Every territorial male was observed for six 30-min periods. The bird's location was recorded during each observation period with a Global Positioning System (GPS) unit at 5-min intervals. Every territorial male was observed for six observation bouts resulting in a minimum of 42 data points. All birds were followed between dawn and 0930 hrs EDT. We used Adaptive Kernel (ADK) to construct territory boundaries (95% ADK) and the "core" territory areas (50% ADK) from each individual's location data (Barg et al. 2005). Territory boundaries and sizes were calculated using CALHOME home range analysis program (Kie et al. 1994).

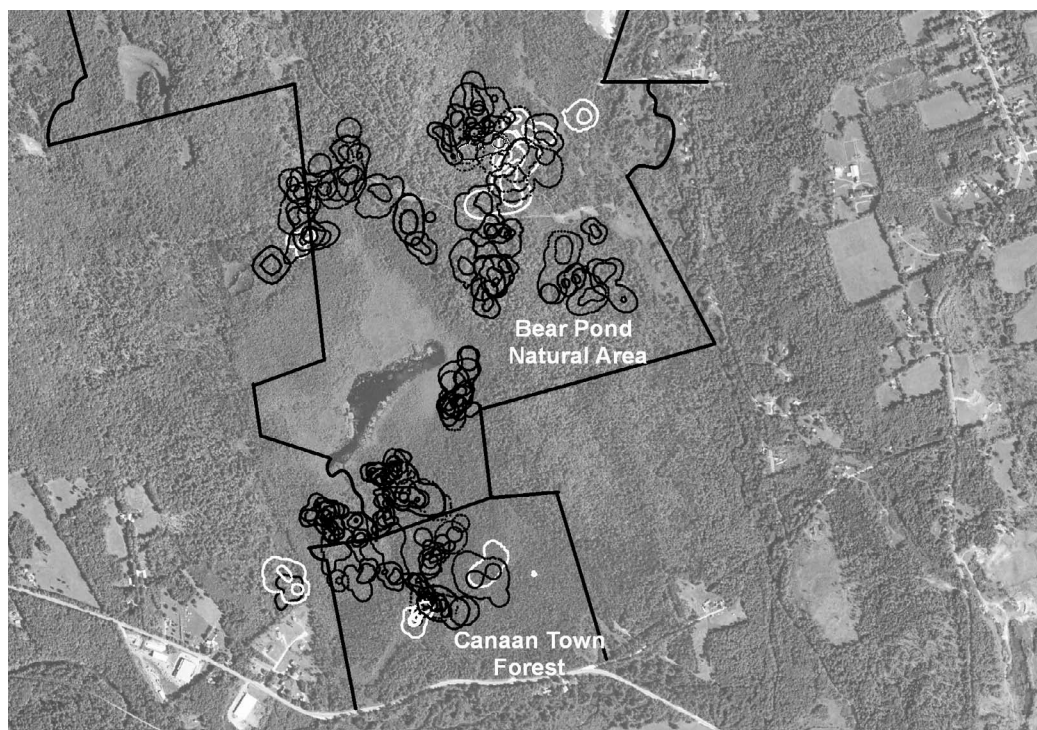


FIG. 1. Canada Warbler territories during 2003–2006 in central New Hampshire used to compare reproductive performance. After-second-year (ASY) male territories are shown in black and second-year (SY) male territories are shown in white. Each territory is the result of an adaptive kernel (ADK) analysis using GPS locations taken during 30-min observation bouts.

Measuring Reproductive Success.—Pairing and fledging success were documented for each male within observation bouts. A male was considered paired if a female was repeatedly detected within his territory. Males singing from high perches throughout the breeding season with no female detected were considered unpaired. A nest on a male's territory was considered successful if at least one fledgling was seen (Howlett and Stutchbury 2003), or if males and females concurrently delivered food to multiple areas within the territory.

Vegetation Sampling.—Minimum convex polygons (MCP) were calculated using CALHOME (Kie et al. 1994) to position up to four vegetation sampling locations on each male's territory. We used MCPs to be consistent with data collected across all years. Only males with the full set of six complete observation bouts were used in vegetation analyses in 2005 and 2006 ($n = 39$ male territories). Ninety-two male territories had a complete set

of six observation bouts from 2003 to 2006 and were used for comparing reproductive success. All vegetation characteristics were quantified using a modification of the Breeding Biology Research and Monitoring [BBIRD] protocol (Martin and Conway 1994). Thirty-nine sets of vegetation plots, each set consisting of 4 subplots, were placed within territories. The position of subplots followed the BBIRD protocol except on territories where subplots had to be shifted to either remain more than 50% within territory boundaries or include actual locations of birds within their territories. If a subplot contained fewer than two observation points or was more than 50% outside of the polygon, it was shifted the least distance possible to meet the criteria. Thirty-two sets of non-territory plots were created using a random number generator and randomly placed in habitat that was not occupied.

We characterized a song perch tree as any

tree that emerged at least 3 m above the surrounding canopy with a radius of >5 m that was not overlapping with the surrounding canopy. These perch sites were presumed to provide high visibility and maximize the distance during singing at which a song may be heard by conspecifics. The density of the shrub foliage was quantified using a pole (2.5 m long and 2.5 cm diameter) marked at half-meter intervals. We recorded the plant species and number of times a branch or leaf touched the pole within each half-meter interval. The pole was placed 1 m from the center of the plot in each of the four cardinal directions. All four subplots for each territory or non-territory analog were averaged for analysis to best approximate the habitat in the area sampled.

Statistical Analyses.—Chi-square analyses were used to compare pairing and fledging success between older (ASY) and younger (SY) males. Fisher's exact test was used to compare age classes of males in 2005 and 2006 on both plots. Wilcoxon signed rank analysis was used, due to non-normal distributions, to compare the territory and core area sizes of older and younger males that had a complete set of observation bouts (42 location points), and to analyze differences in habitat characteristics between the two age classes. Habitat comparisons were made by combining plots to maximize sample size within each age class (Bonferroni adjustments were made for habitat characteristics that were not considered independent, shrub stems: $P < 0.01$, shrub foliage density: $P < 0.01$, tree stems: $P < 0.0083$). We also analyzed age class differences in habitat characteristics within each plot and made the same Bonferroni adjustments for multiple comparisons of variables that were not considered independent.

RESULTS

Ninety-two territories of 71 males over 4 years (2003–2006) were mapped with a complete set of six 30-min observation bouts including 17 males mapped in two consecutive years and four males mapped in three consecutive years. Ninety-three percent of territorial males (66 of 71) were banded. Territories of these marked individuals surrounded unbanded territorial males, making it possible to accurately map the five unmarked individuals. Of the 92 male territories mapped over 4

TABLE 1. Average (\pm SE) territory sizes and core areas (\pm SE) of ASY and SY males in each year calculated by adaptive kernel analysis. These data were based exclusively on males for which a full set of location data points were obtained ($n = 90$). Neither the 4-year average territory sizes nor core areas differed significantly between ASY and SY males.

Age	Year							
	2003		2004		2005		2006	
ASY	Terr.	Core	Terr.	Core	Terr.	Core	Terr.	Core
	1.12 (0.238)	0.249 (0.065)	0.67 (0.140)	0.107 (0.017)	1.11 (0.179)	0.152 (0.036)	1.18 (0.113)	0.232 (0.024)
SY	1.16 One SY	0.150	No SYs in 2004		1.36 (0.165)	0.286 (0.037)	1.27 (0.227)	0.203 (0.041)

TABLE 2. Number (%) of each Canada Warbler age class on each of two plots for each year in west-central New Hampshire during 2003 to 2006.

Age	All males				Territorial males ≥ 30 observations			
	2005		2006		2005		2006	
	Upper	Lower	Upper	Lower	Upper	Lower	Upper	Lower
ASY	11 (52)	14 (82)	24 (83)	17 (77)	9 (64)	13 (87)	21 (81)	17 (85)
SY	10 (48)	3 (18)	5 (17)	5 (23)	5 (36)	2 (13)	5 (19)	3 (15)

years, 76 were defended by ASYs (83%), 14 by SYs (15%), and two by individuals of unknown age (2%). These latter two males were excluded from all analyses (Fig. 1).

The 4-year average (\pm SE) territory size of ASYs (1.07 ± 0.75 ha) did not differ from SYs (1.3 ± 0.23 ha; Wilcoxon signed-rank test: $Z = -1.19$, $P = 0.23$) for the territories for which we had a complete set of six 30-min observation periods on known-aged birds ($n = 90$, Table 1). Similarly, the average ASY core area for the 4 years (0.19 ± 0.14 ha) did not differ from that of SYs (0.23 ± 0.19 ha; Wilcoxon signed-rank test: $Z = -0.89$, $P = 0.37$).

The study area had a clear preponderance of older males (Table 2). A total of 108 male territories had ≥ 30 location observations. Of these 108 males, 91 were ASYs (84%) and 17 were SYs (16%). There were 16 additional territories mapped for which a complete set of six 30-min observation periods was not obtained, and 19 birds that were caught or mapped on the two sites, but not observed again. Of this comprehensive total of 127 birds, 27 were SYs (21.2%). Including these additional captured birds, the proportion of SYs at the red maple swamp site was 15.5% compared to 30% at the early-mid succession site. Age ratios in 2005 and 2006, the years with adequate sample sizes for comparisons, did not differ for all males considered territorial (≥ 30 location observations, Fisher's exact test: $P = 0.215$ in 2005, and $P = 1.00$ in 2006, Table 2).

Reproductive Success.—ASYs paired (96%, 73 of 76) at higher rates than SYs (64%, 9 of 14, $\chi^2 = 14.73$, $df = 1$, $P < 0.001$; Table 3) for all 4 years. However, the proportion of successfully paired males that fledged at least one young did not differ between the two age classes (ASYs = 76.7% [56 of 73], SYs = 67% [6 of 9], $\chi^2 = 0.438$, $df = 1$, $P > 0.05$).

Habitat Characteristics.—Twenty-one habitat characteristics were measured. One of the 21 variables was significantly different between the two age classes when combining both plots and adjusting for multiple comparisons. ASY territories had a significantly lower canopy height than those of SY birds (Wilcoxon signed-rank test: $Z = -2.13$, $P = 0.033$, Table 4). Three habitat characteristics were significantly different between age classes within each plot. On the upper plot, ASYs had significantly more song perch trees per 0.04 ha (average \pm SD for ASYs = 1.98 ± 0.12 vs. 1.41 ± 0.16 for SYs, Wilcoxon signed-rank test: $Z = -2.26$, $P = 0.024$). The total number of shrub stems per 0.00785 ha (5-m radius) was significantly greater on ASY territories (average for ASYs = 42.05 ± 3.41 vs. 26.66 ± 4.05 for SYs, Wilcoxon signed-rank test: $Z = -2.61$, $P = 0.009$). On the lower plot, SYs had significantly more deciduous shrub stems > 2.5 cm dbh (5-m radius) than ASYs (average for ASYs = 2.29 ± 0.32 vs. 10.13 ± 3.40 for SYs, Wilcoxon signed-rank test: $Z = -3.12$, $P = 0.002$).

DISCUSSION

The high proportion of older males in our study area, together with the high overall pairing and fledging success of males over the 4 years for all males combined clearly indicates this is a productive area for the Canada Warbler. ASY males paired at significantly higher rates than SYs, which is consistent with other warbler species, such as the Black-throated Blue Warbler (Holmes et al. 1996) and Ovenbird (Bayne and Hobson 2001). We found that ASY males were more reliably observed throughout the breeding season and a greater proportion were presumed to be territorial based upon observations of males for which we did not have sufficient data to do adaptive kernel analysis. Proportionally fewer SYs per-

TABLE 3. Number (%) of older and younger male Canada Warblers successfully pairing and fledging at least one young in each year at two sites in west-central New Hampshire during 2003 to 2006.

Age	2003		2004 ^a		2005		2006	
	Paired	Fledged	Paired	Fledged	Paired	Fledged	Paired	Fledged
ASY	9/9 (100)	7/9 (78)	11/13 (85)	8/11 (73)	35/36 (97)	28/35 (80)	18/18 (100)	13/18 (72)
SY	0/1	0/0			5/7 (71)	2/5 (40)	4/6 (67)	4/4 (100)

^a No SYs.

sisted throughout the breeding season. However, SYs demonstrated equal success in fledging ≥ 1 young if they were able to maintain a territory and attract a female. Certain SYs were successful in the same years that some ASYs were not. This finding demonstrates impressive variation in individual fitness across age classes. We do not have adequate data at present to analyze whether success as an SY male influences the probability of success in subsequent years.

Differences in pairing success could occur because ASY males may secure territories in habitats that females find more attractive or the males themselves may be more attractive as they are brighter, with bolder necklaces (Rappole 1983), which may signal greater experience. Bold markings have been shown to increase reproductive success of Yellow Warblers (*Dendroica petechia*) (Yezerinac and Weatherhead 1997).

There was no significant difference in size of territories (95% ADK) or core areas (50% ADK) between ASYs and SYs with complete sets of observations. This comparison was based upon combined samples from both plots. In a separate analysis, Hallworth et al. (2008) found that males of both age classes used 50% more area in the upper second-growth plot compared to the lower red maple swamp, but neither reproductive performance nor food abundance differed between the two plots. Territory size is known to vary inversely with food supply in some species (e.g., Stenger 1958). Rodenhouse and Holmes (1992) found that food-rich habitat increases reproductive success for Black-throated Blue Warblers. Paired ASY and SY Canada Warblers did not differ in the rate of fledging at least one young in our study suggesting similar food resources existed in the territories of both age classes, but we did not measure food abundance on territories for each age class of males.

Few habitat characteristics differed between ASY and SY territories. Shrub foliage densities up to 1 m on SY territories were higher than on ASY territories, but not significantly different. Shrub foliage density within this horizon on ASY territories may influence nest site selection in that dense shrubs in the lower stratum may prevent the formation of sphagnum hummocks, a nesting substrate that was

TABLE 4. Habitat characteristics sampled on territories of both ASY and SY male Canada Warblers. All habitat values denote diameter at breast height (dbh), except values under shrub foliage density, where values denote heights. Means \pm SE are shown along with Z and P values with significant differences indicated by an asterisk. Canopy height was the only significantly different vegetative feature. Bonferroni adjustments for shrub stem and foliage densities were both $P = 0.01$, and $P = 0.0083$ for tree stems.

Characteristic	ASY	SY	Z	P
Canopy height, m	7.45 \pm 0.26	8.91 \pm 0.56	-2.130	0.033*
Song posts, 0.04 ha	1.92 \pm 0.10	2.06 \pm 0.25	-0.555	0.579
Sum shrubs	45.20 \pm 2.02	44.55 \pm 3.10	-0.151	0.880
Deciduous shrubs, >1 m				
<2.5 cm	30.46 \pm 2.98	22.17 \pm 3.58	-0.331	0.741
>2.5 cm	6.20 \pm 0.96	5.39 \pm 1.48	-0.238	0.815
Coniferous shrubs, >1 m				
<2.5 cm	10.40 \pm 1.09	8.03 \pm 1.12	-0.506	0.613
>2.5 cm	4.19 \pm 0.33	4.00 \pm 0.61	-0.302	0.763
Shrub foliage density				
0–0.5 m	0.88 \pm 0.20	1.87 \pm 0.48	-2.269	0.023
0.5–1 m	1.13 \pm 0.29	1.73 \pm 0.50	-2.057	0.040
1–1.5 m	1.10 \pm 0.21	1.49 \pm 0.33	-1.793	0.073
1.5–2 m	0.91 \pm 0.13	1.45 \pm 0.28	-1.793	0.073
2–2.5 m	0.94 \pm 0.16	1.71 \pm 0.42	-1.698	0.090
Trees				
Small, 8–22.9 cm	13.30 \pm 0.82	16.43 \pm 2.08	-1.515	0.130
Medium, 23–37.9 cm	2.34 \pm 0.34	2.64 \pm 0.55	-0.813	0.416
Coniferous trees				
Small, 8–22.9 cm	6.69 \pm 0.62	7.33 \pm 1.28	-0.597	0.550
Medium, 23–37.9 cm	0.90 \pm 0.14	1.08 \pm 0.25	-1.165	0.244
Deciduous trees				
Small, 8–22.9 cm	6.51 \pm 0.57	9.05 \pm 1.24	-1.916	0.055
Medium, 23–37.9 cm	1.32 \pm 0.16	1.56 \pm 0.51	-0.80	0.936
Snags				
Sum of all size classes	1.75 \pm 0.22	2.69 \pm 0.86	-0.929	0.353
Small, 8–22.9 cm	1.59 \pm 0.22	2.48 \pm 0.85	-0.831	0.406
Medium, 23–37.9 cm	0.16 \pm 0.04	0.20 \pm 0.09	-0.845	0.398

common if not preferred (Conway 1999, this study). Twelve of 18 nests found in 2005 and 2006 were within sphagnum hummocks, and were among the most cryptic of nest locations. In contrast, greater shrub cover on SY territories may inhibit the ability of predators from locating nests (Bowman and Harris 1980).

Average canopy height was significantly lower within ASY territories compared to SY territories. The lower canopy height on ASY territories for both plots may factor into female assessment of prospective mates. We found that ASYs had more song perch trees and total shrub stem densities on the upper, second-growth plot in the single-plot habitat analyses between age classes. The greater

number of emergent perch sites and higher total shrub stem densities in this second-growth may combine to attract females more frequently to ASY territories, which is consistent with the higher pairing success of ASYs in our study. Larger shrubs (>2.5 cm dbh) were more abundant on SY territories on the lower, red maple swamp plot. ASYs occupied most of the dense deciduous thickets typical of red maple swamp on the lower plot. These dense thickets tended to have stems <2.5 cm dbh, whereas peripheral areas had larger-stemmed shrubs. The latter was more typical of SY territories on the lower plot.

The habitat complex in which this study was conducted is presumed to be of high qual-

ity given the high ASY: SY ratio (Hunt 1996) and reproductive success (Holmes et al. 1996) of territory-holders. More work needs to be done to compare ASY and SY reproductive performance in areas with different demographic ratios assuming that within-population differences are likely to be more pronounced in more marginal habitat.

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